ZOOLOGIA 36: e32138
ISSN 1984-4689 (online)
zoologia.pensoft.net

RESEARCH ARTICLE

Hybridism between *Cyanocorax chrysops* and *Cyanocorax cyanopogon* (Aves: Corvidae) in Brazil

Cristiane Apolinario[1], **Luís Fábio Silveira**[1]

[1]*Museu de Zoologia da Universidade de São Paulo. Avenida Nazaré 481, Ipiranga, 04263-000 São Paulo, SP, Brazil.*
*Corresponding author: Cristiane Apolinario (*cris.snt4@gmail.com*)*

http://zoobank.org/27929D4C-8CBD-45C8-AB27-28816EDE5BED

ABSTRACT. *Cyanocorax chrysops* (Vieillot, 1818) and *Cyanocorax cyanopogon* (Wied, 1821) are widespread jays. They are considered sister species according to recent molecular phylogenies. When analyzing museum specimens of both species, we found two individuals with intermediate plumage characteristics. They were collected near the range limits of both species, and we classified them as hybrids. Based on the sites where these specimens were found, we discuss the possible factors leading the interbreeding and compare our findings with information available in the literature. This is the first documented case of natural hybridization in jays in Brazil and the second case involving sister species within the New World jays.

KEY WORDS. Contact zones, hybrids, interbreeding, jays.

INTRODUCTION

Hybridization is a phenomenon of basic relevance in biology (McCarthy 2006), and zoologists have often considered it a sporadic event (Mayr 1963). Hybridization, the mating between two different species that results in offspring, might be considered a rare phenomenon because it is geographically restricted and because hybrids represent between 0.1 and 5% of populations (Mallet 2005, Arnold 1997, 2006). Nevertheless, it has been suggested that about 10% of all animal species hybridize naturally (Mallet 2005). With the advance of molecular techniques, the number of reports on natural hybridization and hybrid speciation has increased in the past decades (Brelsford 2011).

Hybridization can occur in a contact zone, there is, in areas where the ranges of two populations overlap; and those can become a hybrid zone, where hybridization occurs regularly (McCarthy 2006). A hybrid can be defined as an individual mixing the physical traits of individuals of two different but not necessarily related taxa. Hybrids can express the traits of their parents in three ways: combination, when a trait resembles only one of the parents; intermediacy, when the traits seem to express a mix between the parents; and heterotic, when the hybrid presents a trait well outside of the range of parental variation (McCarthy 2006).

McCarthy (2006) listed all reported cases of hybridization in the family Corvidae. In this family, natural hybridization is rare (Pitelka et al. 1956). Even so, one of the most complex case of hybridization involves the interbreeding between *Corvus corone corone* Linnaeus, 1758 and *Corvus corone cornix* Linnaeus, 1758 with an extensive hybrid zone (Picozzi 1976, Rolando 1993, Haas et al. 2009, Wolf et al. 2010, Brodin et al. 2013).

New World jays do not hybridize as often or as extensively as Old-World ones. Some records mention occasional hybridization involving congeneric species, for instance *Cyanocorax morio* (Wagler, 1829) and *Cyanocorax formosus* (Swainson, 1827) (Pitelka et al. 1956), two morphologically distinct species, whereas others involve hybridization between sister species, for example *C. formosus* and *Cyanocorax colliei* (Vigors, 1829) (McCarthy 2006, Anjos and de Juana 2018) and *Cyanocitta cristata* (Linnaeus, 1758) and *Cyanocitta stelleri* (Gmelin, 1788) (Williams and Wheat 1971). Hybridization in captivity has also been observed, comprising almost half of the known cases, more often when there is no conspecific individual to pair up with (Hardy and Wheat 1982), for instance between *Cyanocorax yncas* (Boddaert, 1783) and *C. cristata* (Pulich and Dellinger, 1981).

The Neotropical jays belonging to the genus *Cyanocorax* Boie, 1826 comprise a very distinct group of New World corvids. *Cyanocorax chrysops* (Vieillot, 1818), the Plush-crested Jay, is a polytypic species widely distributed in South America, ranging from northern Brazil to northern Argentina, with four subspecies currently accepted: *C. c. chrysops* (Vieillot, 1818), *C. c. diesingii* Pelzeln, 1856, *C. c. insperatus* Pinto and Camargo, 1961 and *C. c. tucumanus* Cabanis, 1883. This species is found in various types of lowland forests and temperate rainforest, also inhabiting patches

of forest in open areas, riparian forests and even disturbed areas. *Cyanocorax cyanopogon* (Wied, 1821), the White-naped Jay, in turn, inhabits mostly areas of 'caatinga' and 'cerrado', but it is also seen in secondary woodland, riparian forests, and in the borders of tropical deciduous forests. It is Brazilian endemic, distributed from the state of Maranhão to the state of Minas Gerais, also occurring in southeastern Pará, eastern Mato Grosso and Goiás (Madge and Burn 1994, Anjos et al. 2009, 2019a, b). Regarding the preferences of habitat occupancy, *C. chrysops* prefers to occupy the understory and the middle level, exhibiting some variation in habitat use (Uejima et al. 2012). On the contrary, the unique information available about the preferences of *C. cyanopogon* is the use of the ground when foraging (Barros et al. 2014). The information about the reproductive behavior of both species is very limited (Uejima et al. 2012).

Cyanocorax chrysops and *C. cyanopogon* are considered sister species (Bonaccorso et al. 2010) and due their morphological similarity they have been previously treated as conspecific (Pinto 1954, Pinto and Camargo 1961, Blake and Vaurie 1962). In addition, Pinto (1954) described a taxon based on a single specimen from Alagoas, *Cyanocorax chrysops interpositus*, considering it as an intermediate form between the two species. Later, Hardy (1969) questioned the validity of *C. c. interpositus*, arguing that the specimens assigned to this subspecies were actually molting, worn, and subadults of *C. cyanopogon*, discarding its intermediate position both in geographic and genetic sense. There are no reliable records or specimens confirming the existence of intermediate individuals between the two so far, but we found two museum specimens showing intermediate plumage patterns between *C. chrysops* and *C. cyanopogon* from two different sites in Brazil, which we identified as hybrids. Thus, our objectives were to describe these hybrid specimens and discuss the possible causes behind the interbreeding and the existence of contact zones.

MATERIAL AND METHODS

We analyzed 80 specimens of *C. chrysops* and 137 of *C. cyanopogon* housed at Museu de Zoologia da Universidade de São Paulo (MZUSP) and Museu Paraense Emílio Goeldi (MPEG) (see Supplementary Material S1) in order to describe the plumage pattern of each hybrid and then compare it with the plumage of their parents. We analyzed plumage coloration following Smithe (1975) and Munsell (1994) color catalogues (hereafter S and M, respectively). In addition, we also analyzed records of both species on the Brazilian online database WikiAves (http://wikiaves.com.br) aiming to delimit a more precise range limit of both taxa, trying to identify putative contact zone areas.

RESULTS

We found two specimens, one from Três Lagoas, state of Mato Grosso do Sul (MZUSP 64191), and a second from Comendador Gomes, state of Minas Gerais (MZUSP 103009), showing intermediate plumage characters between *C. cyanopogon* and the nominate form *C. c. chrysops*. The most remarkable plumage characters exhibited by these particular specimens were: (1) back and wings dark grayish brown, (2) tail indigo blue or dark grayish brown + indigo blue and (3) nape light bluish gray/dull violaceous blue or white/lavender blue (Table 1). The main difference between the two is that the specimen from Três Lagoas has yellowish underparts whereas the specimen from Comendador Gomes shows white underparts, with each one being more similar to one of its parental species, resembling *C. c. chrysops* and *C. cyanopogon*, respectively. Following the classification given by McCarthy (2006), the hybrids showed both, intermediate traits (characters 1 and 3 in both hybrids and character 2 in the hybrid 2) and a combined trait (character 2 in the hybrid 1).

There are specimens of both species from Três Lagoas, *C. c. chrysops* (MZUSP 64192) and *C. cyanopogon* (MZUSP 73779) (Figs 1–3) in addition to records from WikiAves database; WA12379 (*C. c. chrysops*) and WA 3230616 (*C. cyanopogon*). The existence of these specimens and records demonstrates that parental forms come into contact in this region, one of the prerogatives to designate a true hybrid according to McCarthy (2006). Otherwise, in Comendador Gomes, a place near the São Paulo border, there are no specimens or records of both species rather than the hybrid.

DISCUSSION

Identifying the causes of hybridization requires understanding how ecology, demography and phenotype influence mate choice in a particular species (Willis 2013). Many factors could be involved in hybridization, but environment and behavior are known to be the main drivers causing this phenomenon (McCarthy 2006, Randler 2006); however, a close genetic relationship is considered an important factor leading to it (Randler 2006). In fact, it is been argued that species with small genetic distances are more prone to hybridize (Gholamhosseini et al. 2013), and sister taxa tend to interbreed more than non-sister taxa due their similar morphology (Randler 2002, 2004, 2006). There is no doubt about the close relationship between *C. chrysops* and *C. cyanopogon* based on morphology and molecular studies (Bonaccorso et al. 2010). Not only morphological similarity, but similarity in mating signals might be also a significant factor inducing interspecific pairing and hybridization (Gholamhosseini et al. 2013) and even the voice repertoire of the two seems to be very similar (Anjos 2019a), which would facilitate recognition of mating signals. The case of *C. chrysops* and *C. cyanopogon* match all these statements, revealing that multiple and related factors are involved and could be used to explain why they hybridize.

McCarthy (2006) pointed to breeding range overlap between *C. chrysops* and *C. cyanopogon* in southern Pará, but no specimen was mentioned or was found by us to substantiate his statement. Willis (1992), in turn, believed that the two taxa meet in western São Paulo, while Madge and Burn (1994) asserted that

Table 1. Comparison of plumage characters of the hybrids between *Cyanocorax chrysops chrysops* and *Cyanocorax cyanopogon*.

Character	*C. c. chrysops*	Hybrid 1 (MZUSP 64191)	Hybrid 2 (MZUSP 103009)	*C. cyanopogon*
Nape	Light sky blue (S 168D)/Campanula (S 71)	Light bluish Gray (M 10B 8/1)/Dull violaceous blue (S 170B)	White (M 2.5Y 8/1)/Lavender blue (S 170D)	White (M 2.5Y 8/1)
Superciliar spot	Smalt blue (S 170)/Light Sky blue (S 168D)	Smalt blue (S 170)/Light Sky blue (S 168D)	Light Sky blue (S 168D)	Light Sky blue (S 168D)
Malar spot	Campanula (S 71)	Campanula (S 71)	Smalt blue (S 70)	Cyanine blue (S 74)
Infraocular spot	Smalt blue (S 170)	Smalt blue (S 170)	Smalt blue (S 170)	Smalt blue (S 170)
Abdomen and underparts	Pale Yellow (M 2.5Y 8/3)	Pale Yellow (M 2.5Y 8/3)	White (M 2.5Y 8/1)	White (M 2.5Y 8/1)
Central rectrices and outer vanes of lateral rectrices	Indigo Blue (S 73)	Indigo Blue (S 73)	Dark grayish brown (S 20) + Indigo blue (S 173)	Sepia (S 119)
Rectrices tips	Pale Yellow (M 2.5Y 8/3)	Pale Yellow (M 2.5Y 8/3)	White (M 2.5Y 8/1)	White (M 2.5Y 8/1)
Back, rump and wing coverts	Indigo blue (S 73)	Dark grayish Brown (S 20)	Dark grayish Brown (S 20)	Sepia (S 119)

Figures 1–3. Hybrid MZUSP 64191 (2) between *C. c. chrysops* MZUSP 26041 (1) and *C. cyanopogon* MZUSP 27910 (3). Back and wings are brownish, resembling *C. cyanopogon*. The crest feathers have the typical *C. c. chrysops* shape, but nape coloration is lighter, almost completely white like *C. cyanopogon*.

the two species meet in eastern Mato Grosso. Our findings agree with Willis (1992) since one of the specimens was collected at the border between the states of Mato Grosso do Sul and São Paulo (Fig. 4). Moreover, it is possible to identify two conspicuous areas where the ranges of both species overlap: southern Minas Gerais and eastern Mato Grosso do Sul, the very same areas where we found the hybrid specimens. However, eastern Mato Grosso and Pará could be potential contact areas due the proximity of the range limits of both taxa, especially for *C. c. diesingii*, which shows an easternmost record very close to the westernmost records of *C. cyanopogon*, and because *C. c. diesingii* inhabits patches of open drier vegetation (Pacheco and Olmos 2005, Lees et al. 2008, Anjos et al. 2009, Whittaker 2009, Olmos et al. 2011, Santos et al. 2011), environments very similar to those inhabited by *C. cyanopogon*.

We are not able to ascertain if there is a stable hybrid zone, and there is no information about an area where individuals of *C. chrysops* and *C. cyanopogon* interbreed regularly. Possible reasons for the paucity of records of intermediate individuals could come from the great similarity of the parental species, which are often erroneously identified: individuals of *C. chrysops* are misidentified as *C. cyanopogon* and vice-versa. When the parental taxa are similar, the phenotype of the offspring produced by hybridization might be also more similar to one of the parents, making it difficult to identify visually as intermediate so they could just have remained unnoticed. On the other hand, the lack of intermediate individuals could just reflect the rarity of the interbreeding, as hybridization between other species of *Cyanocorax* is rare. For instance, *C. chrysops* is sympatric with other congeneric species, *C. cyanomelas* (Vieillot, 1818) and *C. caeruleus*

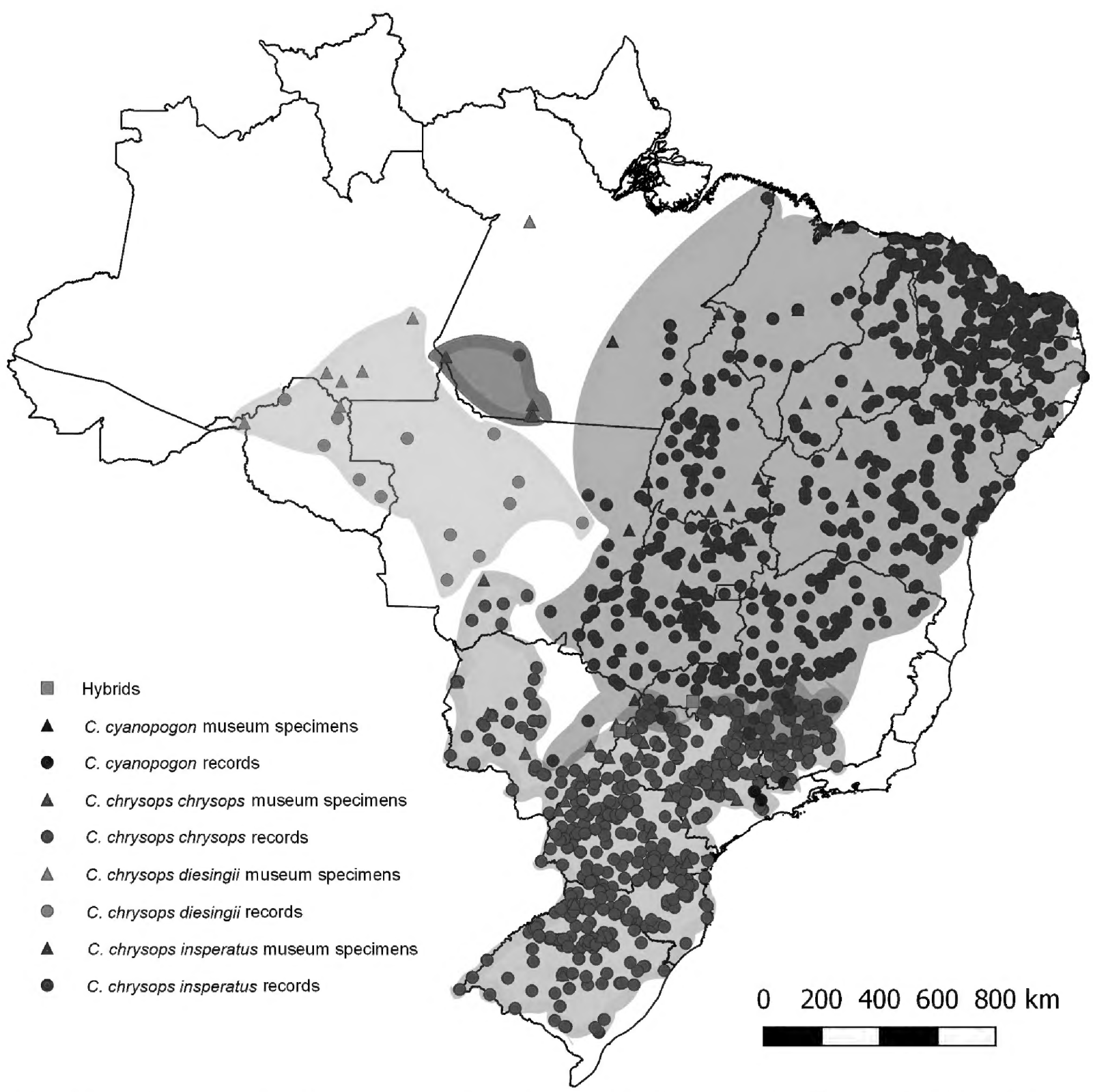

Figure 4. Distribution of *C. chrysops* and *C. cyanopogon* based on specimens analyzed and WikiAves' photographic records. Triangles represent the specimens and circles the photos analyzed.

(Vieillot, 1818) in part of its range (Goodwin 1976, Madge and Burn 1994) and there is no evidence of hybridism between these species, which have a dissimilar morphology when compared to *C. chrysops*, also demonstrating that sympatry by itself may not be a factor leading to hybridization. Thus, without any other clear indication and based on data we have, we suppose that hybridization between the two taxa occurs only occasionally in contact zones.

Hybridization is more common in areas where two related species meet and one of them is rarer. Thus, restricted mate choice drives the interbreeding (Hubbs 1955, Mayr 1967, Short 1969, Gillespie 1985, Grant and Grant 1997, Wirtz 1999, 2000). In the absence of conspecifics, individuals have to "choose" between mating heterospecifically or not mating at all (Randler 2006), a hypothesis known as "making the best of a bad job" (Baker 1996). The occurrence of *C. cyanopogon* in Mato Grosso do Sul is rare (Godoi et al. 2013), and there are only three municipalities where this species was recorded in WikiAves database. Otherwise, there are several records of *C. chrysops* and museum specimens from the same state, proving that it is the commonest species there. On the other hand, in southwestern Minas Gerais both species seem to be uncommon, as *C. cyanopogon* is considered rare in northern São Paulo (Anjos 2019a), and *C. chrysops* is known by a handful of records in the same region.

Deforestation and habitat modification affect the range of the species, and those inhabiting non-forest environments are expanding their distribution throughout Brazil, for instance *Patagioenas picazuro* (Temminck, 1813) (Willis and Oniki 1987), *Ramphastos toco* Statius Müller, 1776 (Sick 1997), *Rhynchotus rufescens* (Temminck, 1815) (Willis and Oniki 2002), and *Cyanocorax cristatellus* (Temminck, 1823) (Lopes 2008). One of the effects of range expansions is that it increases the possibility of taxa coming into secondary contact due the lack of a natural barrier. For instance, an invading species, initially rare locally, might mate heterospecifically because conspecific partners are at low frequency (Rheindt and Edwards 2011, Duckworth and Semenov 2017). The same occurs in transitional zones, which often show disparities in the relative abundances of species (Jansson et al. 2007, Lepais et al. 2009, Larson et al. 2013). *Cyanocorax cyanopogon* is expanding its range southward due the habitat modification, reaching the state of Espírito Santo (Anjos 2019a). The range of *C. chrysops*, in turn, does not seem to be expanding. This species is not very vulnerable to habitat fragmentation, being present in urban areas in southern and southeastern Brazil (Anjos 2019b). *Cyanocorax cyanopogon* and *C. chrysops* have a very diverse diet (Madge and Burn 1994, Anjos et al. 2009, Barros et al. 2014) and exhibit plasticity and differences in habitat use (Uejima et al. 2012, Barros et al. 2014). Therefore, they probably do not compete for resources when co-occurring, so that these features also contribute to the ability of individuals to persist in disturbed or transitional areas.

The two sites where the hybrids were collected are transitional areas from drier vegetation formations (Cerrado, southwestern Minas Gerais and eastern Mato Grosso do Sul) to areas of humid forests (western São Paulo), and this may explain the differences in abundance of both species, easing the possibility of hybridization. Moreover, with the advance of deforestation, we detected putative new contact areas. Both species were recorded on some urban surroundings in the cities of Araxá (WA 1333137 and WA 745949), Belo Horizonte (WA 2006717 and WA 47372) in Minas Gerais, and Meridiano (WA 1702233 and WA 775584) in São Paulo state, showing that *C. chrysops* and *C. cyanopogon* can also meet in very modified environments and new events of hybridization are likely to occur.

In summary, the best predictors to explain the occurrence of hybrids between *C. chrysops* and *C. cyanopogon* are those from morphological and behavior similarity coupled with a putative rarity of conspecific pairs. Our findings highlight the need to conduct further studies in areas of range overlap to investigate the rate and frequency of hybridization and its consequences for the genetic integrity of the species involved.

ACKNOWLEDGEMENTS

We thank Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) (grant 2013/22026-1). LFS is supported by Conselho Nacional de Desenvolvimento Cientifico e Tecnológico research productivity fellowship (process #302291/2015-6). We are thankful to Alexandre Aleixo (MPEG) for the specimens' loan and Gustavo Bravo for assisting with the procedures associated with the loan. Thiago Costa and two anonymous reviewers helped us to improve an earlier version of this manuscript.

LITERATURE CITED

Anjos L, Debus S, Madge S, Marzluff JM (2009) Family Corvidae. Species accounts. In: del Hoyo J, Elliott A, Christie DA (Eds) Handbook of the birds of the world. Barcelona, Lynx Edicions, vol. 14, 566–640.

Anjos L, de Juana E (2018) Black-throated Magpie-jay (*Cyanocorax colliei*). In: del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E (Eds) Handbook of the birds of the world alive. Barcelona. Lynx Edicions, https://www.hbw.com/node/60724 [Accessed: 20/11/2018]

Anjos L (2019a) White-naped Jay (*Cyanocorax cyanopogon*). In: del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E (Eds) Handbook of the birds of the world alive. Barcelona, Lynx Edicions, https://www.hbw.com/node/60722 [Accessed: 10/04/2019]

Anjos L (2019b) Plush-crested Jay (*Cyanocorax chrysops*). In: del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E (Eds) Handbook of the birds of the world alive. Barcelona, Lynx Edicions, https://www.hbw.com/node/60721 [Accessed: 10/04/2019]

Arnold ML (1997) Natural hybridization and evolution. New York, Oxford University Press, 232 pp.

Arnold ML (2006) Evolution through genetic exchange. New York, Oxford University Press, 272 pp.

Baker MC (1996) Female buntings from hybridizing populations prefer conspecific males. The Wilson Bulletin 108: 771–775. https://www.jstor.org/stable/4163756

Barros RAM, Costa CA, Pascotto MC (2014) Diet and feeding behavior of the White-naped Jay, *Cyanocorax cyanopogon* (Wied, 1821) (Aves, Passeriformes, Corvidae) in a disturbed environment in central Brazil. Brazilian Journal of Biology 74(4): 899–905. https://doi.org/10.1590/1519-6984.09313

Blake ER, Vaurie C (1962) Corvidae. In: Mayr E, Greenway JC (Eds) Peters' check-list of birds of the world. Cambridge, Museum of Comparative Zoology, vol. 15, 204–282.

Bonaccorso E, Peterson AT, Navarro-Sigüenza AG, Fleischer RC (2010) Molecular systematics and evolution of the *Cyanocorax* jays. Molecular Phylogenetics and Evolution 54(3): 897–909. https://doi.org/10.1016/j.ympev.2009.11.014

Brelsford A (2011) Hybrid speciation in birds: allopatry more important than ecology? Molecular Ecology 20: 3705–3707. https://doi.org/10.1111/j.1365-294X.2011.05230.x

Brodin A, Haas F, Hansson B (2013) Gene flow across the European crow hybrid zone – a spatial simulation. Journal of avian Biology 44(3): 281–287. https://doi.org/10.1111/j.1600-048X.2012.00017.x

Duckworth RA, Semenov GA (2017) Hybridization associated with cycles of ecological succession in a passerine bird. The American Naturalist 190(4): E94–E105. https://doi.org/10.1086/693160

Gillespie GD (1985) Hybridization, introgression, and morphometric differentiation between mallard (*Anas platyrhynchos*) and grey duck (*Anas superciliosa*) in Otago, New Zealand. Auk 102: 459–469. https://www.jstor.org/stable/4086641

Gholamhosseini A, Vardakis M, Aliabadian M, Nijman V, Vonk R (2013) Hybridization between sister taxa versus non-sister taxa: a case study in birds. Bird Study 60(2): 195–201. https://doi.org/10.1080/00063657.2013.770815

Godoi MN, Morante-Filho JC, Módena ÉS, Faxina C, Tizianel FAT, Bocchese R, Pivatto MAC, Nunes AP, Posso SR (2013) Birds of upper Paraná River basin in the state of Mato Grosso do Sul, Brazil. Revista Brasileira de Ornitologia 21(3): 176–204.

Goodwin D (1976) Crows of the world. Ithaca, Cornell University Press, 354 pp.

Grant PR, Grant BR (1997) Hybridization, sexual imprinting, and mate choice. The American Naturalist 149: 1–28. https://doi.org/10.1086/285976

Haas F, Pointer MA, Saino N, Brodin A, Mundy NI, Hansson B (2009) An analysis of population genetic differentiation and genotype-phenotype association across the hybrid zone of carrion and hooded crows using microsatellites and MC1R. Molecular Ecology 18(2): 294–305. https://doi.org/10.1111/j.1365-294X.2008.04017.x

Hardy JW (1969) A taxonomic revision of the New World jays. The Condor 71(4): 360–375. https://www.jstor.org/stable/1365735

Hardy JW, Wheat P (1982) Vocalisations and other characteristics of Blue and Steller's jays and their hybrids. Bird Behavior 4(1): 21 29. https://doi.org/10.3727/015613882791560567

Hubbs CL (1955) Hybridization between fish species in nature. Systematic Zoology 4: 1–20. https://www.jstor.org/stable/2411933

Jansson G, Thulin C-G, Pehrson Å (2007) Factors related to the occurrence of hybrids between brown hares *Lepus europaeus* and mountain hares *L. timidus* in Sweden. Ecography 30: 709–715. https://doi.org/10.1111/j.2007.0906-7590.05162.x

Larson EL, Becker CG, Bondra ER, Harrison RG (2013). Structure of a mosaic hybrid zone between the field crickets *Gryllus firmus* and *G. pennsylvanicus*. Ecology and Evolution 3(4): 985–1002. https://doi.org/10.1002/ece3.514

Lees AC, Davis BJ, Oliveira AVG, Peres CA (2008) Avifauna of a structurally heterogeneous forest landscape in the Serra dos Caiabis, Mato Grosso, Brazil: a preliminary assessment. Cotinga 29: 149–159. http://e-space.mmu.ac.uk/id/eprint/617294

Lepais O, Petit RJ, Guichoux E, Lavabre JE, Alberto F, Kremer A, Gerber S (2009) Species relative abundance and direction of introgression in oaks. Molecular Ecology 18: 2228–2242. https://doi.org/10.1111/j.1365-294X.2009.04137.x

Lopes LE (2008) The range of the Curl crested Jay: lessons for evaluating bird endemism in the South American Cerrado. Diversity and Distributions 14(4): 561–568. https://doi.org/10.1111/j.1472-4642.2007.00441.x

Madge S, Burn H (1994) Crows and Jays: A guide to the crows, jays, and magpies of the world. Boston, Houghton Mifflin Co., 256 pp.

Mallet J (2005) Hybridization as an invasion of the genome. Trends in Ecology & Evolution 20: 229–237. https://doi.org/10.1016/j.tree.2005.02.010

Mayr E (1963) The breakdown of isolating mechanisms (hybridisation) In: Mayr E (Ed.) Animal species and evolution. Cambridge, Belknap Press, 110–135.

Mayr E (1967) Artbegriff und Evolution. Hamburg, Paul Parey, 617 pp.

McCarthy EM (2006) Handbook of avian hybrids of the world. New York, Oxford University Press, 602 pp.

Munsell (1994) Soil, color charts, revised edition. New Windsor, Macbeth Division of Kollmorgan Instruments Corporation.

Olmos F, Silveira LF, Benedicto GA (2011) A Contribution to the ornithology of Rondônia, southwest of the Brazilian Amazon. Revista Brasileira de Ornitologia 19(44): 200–229.

Pacheco JF, Olmos F (2005) Birds of a latitudinal transect in the Tapajós-Xingu interfluvium, eastern Brazilian Amazonia. Revista Brasileira de Ornitologia 13(22): 29–43.

Picozzi N (1976) Hybridization of carrion and hooded crows *Corvus c. corone* and *Corvus c. cornix*, in northeastern Scotland. Ibis 118(2): 254–257. https://doi.org/10.1111/j.1474-919X.1976.tb03072.x

Pinto O (1954) Resultados ornitológicos de duas viagens científicas ao estado de Alagoas. Papéis do Departamento de Zoologia 12(1): 1–98.

Pinto OM, Camargo EA (1961) Resultado ornitológico de quatro recentes expedições do Departamento de Zoologia no nordeste do Brasil, com a descrição de seis novas subespécies. Arquivos de Zoologia de São Paulo 11: 193–284.

Pitelka FA, Selander RK, del Toro MA (1956) A hybrid jay from Chiapas, Mexico. The Condor 58(2): 98–106. https://www.jstor.org/stable/1364976

Pulich WM, Dellinger RM (1981) An example of a hybrid Green jay × Blue jay. The Wilson Bulletin 93(4): 538–540. https://www.jstor.org/stable/4161546

Randler C (2002) Avian hybridization, mixed pairing and female choice. Animal Behaviour 63: 103–119. https://doi.org/10.1006/anbe.2001.1884

Randler C (2004) Frequency of bird hybrids: does detectability make all the difference? Journal of Ornithology 145: 123–128. https://doi.org/10.1007/s10336-004-0022-0

Randler C (2006) Behavioural and ecological correlates of natural hybridization in birds. Ibis 148(3): 459–467. https://doi.org/10.1111/j.1474-919X.2006.00548.x

Rheindt FE, Edwards SV (2011) Genetic introgression: an integral but neglected component of speciation in birds. Auk 128: 620–632. https://doi.org/10.1525/auk.2011.128.4.620

Rolando A (1993) A study on the hybridization between Carrion and Hooded Crow in Northwestern Italy. Ornis Scandinavica 24(1): 80–83. https://www.jstor.org/stable/3676414

Santos MPD, Silveira LF, Silva JMC (2011) Birds of Serra do Cachimbo, Para state, Brazil. Revista Brasileira de Ornitologia 19(2): 244–259.

Short LL (1969) Taxonomic aspects of avian hybridization. Auk 86(1): 84–105. https://www.jstor.org/stable/4083543

Sick H (1997) Ornitologia brasileira. Rio de Janiero, Editora Nova Fronteira, 862 pp.

Smithe FB (1975) Naturalist's color guide. New York, American Museum of Natural History, 229 pp.

Uejima AMK, Boesing AL, Anjos LD (2012) Breeding and foraging variation of the Plush-crested Jay (*Cyanocorax chrysops*) in the brazilian Atlantic Forest. The Wilson Journal of Ornithology 124(1): 87–95. https://doi.org/10.2307/41932804

Whittaker A (2009) Pousada Rio Roosevelt: a provisional avifaunal inventory in south-western Amazonian Brazil, with information on life history, new distributional data and comments on taxonomy. Cotinga 31: 20–43.

Williams O, Wheat P (1971) Hybrid jays in Colorado. Wilson Bulletin 83: 343–346.

Willis EO, Oniki Y (1987) Invasions of deforested regions of São Paulo state by the Picazuro Pigeon, *Columba picazuro* Temminck, 1813. Ciência e Cultura 39: 1064–1065.

Willis EO (1992) Zoogeographical origins of eastern Brazilian birds. Ornitología Neotropical 3: 1–15.

Willis EO, Oniki Y (2002) Birds of Santa Teresa, Espírito Santo, Brazil: do humans add or subtract species? Papéis Avulsos de Zoologia 42: 193–264. https://doi.org/10.1590/S0031-10492002000900001

Willis PM (2013) Why do animals hybridize? Acta Ethologica 16(3): 127–134. https://doi.org/10.1007/s10211-013-0144-6

Wirtz P (1999) Mother species-father species: unidirectional hybridization in animals with female choice. Animal Behaviour 58: 1–12. https://doi.org/10.1006/anbe.1999.1144

Wirtz P (2000) Einseitige hybridisierung im tierreich. Naturwissenschaftliche Rundschau 53: 172–175.

Wolf JB, Bayer T, Haubold B, Schilhabel M, Rosenstiel P, Tautz D (2010) Nucleotide divergence vs. gene expression differentiation: comparative transcriptome sequencing in natural isolates from the carrion crow and its hybrid zone with the hooded crow. Molecular Ecology 19: 162–175. https://doi.org/10.1111/j.1365-294X.2009.04471.x

Submitted: December 3, 2018
Accepted: April 28, 2019
Available online: September 16, 2019
Editorial responsibility: Sionei Ricardo Bonatto

Author Contributions: CA and LFS contributed equally to this article.
Competing Interests: The authors have declared that no competing interests exist.